LIVING CASSIDULOIDS (ECHINODERMATA: ECHINOIDEA): A KEY AND ANNOTATED LIST

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Abstract. — A key to the 30 known living species of cassiduloids is provided which includes abbreviated geographic and bathymetric data. All species are illustrated for the first time in a single work. An annotated list of genera and species includes basic taxonomic information, remarks upon systematic affinities, more detailed discussions of geographic and bathymetric ranges, and summaries of general biology and habitat preferences.

The order Cassiduloida (sensu Kier 1962) consists of some 800 species of irregular echinoids, most of which are known only as fossils. Kier (1962:1) characterized this order as comprising "all those 'irregular' echinoids having petals, phyllodes, and bourrelets (the floscelle)." However, this general description also applies to such forms as clypeasteroids, which have not only well-developed petaloids, but also what can be interpreted as floscelles consisting of inter-ambulacral bourrelets and reduced phyllodes with buccal and large food groove podia (sensu Mooi 1986). This, along with great variation in the major features used to characterize the families within the order Cassiduloida (for example, the periproct varies in position from aboral and in a deep groove to submarginal), renders it difficult to unambiguously define the order Cassiduloida without using features common to other major irregular echinoid groups. Lack of unique unifying characters leads to suspicions that the group is not monophyletic. I am at present preparing a phylogenetic revision of the living cassiduloid species that should shed light on this problem. In spite of the possibility that the Cassiduloida as defined by Kier (1962) may not be a natural group, it remains convenient to refer to this assemblage as the "cassiduloids." For the purposes of this paper, this group includes all those shallow burrowing irregular echinoids with a relatively high test, short spines, a posteriorly placed periproct, and well-developed floscelle.

Although abundant as Mesozoic and Cenozoic fossils, the cassiduloids have dramatically decreased in number since the Eocene (Kier 1974, Suter 1988). Studies of the pattern of decline of the cassiduloids (Suter 1988) and the evolution of other major irregular echinoid groups (Mooi 1987) have made desirable a review of the distinguishing features of, and basic biological information on, the Recent taxa of the Cassiduloida. In his monograph of the echinoids, Mortensen (1948) listed 27 Recent species of cassiduloids, including the 5 species in the Neolampadidae which he thought constituted a separate family within the order. Since Mortensen's work, three new species of cassiduloids have been described (Krau 1954, Baker 1983, Mooi 1990), and additional morphological and biogeographic information has become available, particularly for the poorly known neolampadids (McKnight 1968). Kier (1962) never mentioned the Neolampadidae in his revision of the Cassiduloida and did not offer a reason for their exclusion. Although Philip (1963) raised the family Neolampadidae to subordinal rank (Neolampadina) within the Cassiduloida, only its familial

standing is recognized here, pending phylogenetic revision of the living taxa in the order.

The most recent key to the cassiduloids is that of Mortensen (1948). In light of information accumulated over the past 40 years, a new, illustrated key to the living species of the group is needed. The key and annotated list include the neolampadids and the cassiduloid genus *Oligopodia,* which Kier (1962) also omitted from his revision. For the first time in a single work, all the known Recent species are figured. I have included brief comments on taxonomy, affinities, and geographic and bathymetric ranges as well as a summary of what has become known of the biology of some of the species since Mortensen (1948).

List of Recognized Taxa

Phylum Echinodermata Bruguière, 1789
  Subphylum Echinozoa Haeckel in Zittel, 1895
    Class Echinoidea Leske, 1778
      Subclass Euechinoïdea Bronn, 1860
        Infraclass Acroechinoidea A. B. Smith, 1981
          Cohort Irregularia Latreille, 1825
            Superorder Microstomata A. B. Smith, 1984
              Series Neognathostomata A. B. Smith, 1981
                Order Cassiduloida Claus, 1880
                  Family Echinolampadidae Gray, 1851
                    Genus *Echinolampas* Gray, 1825
                      Echinolampas ovata (Leske, 1778)
                      Echinolampas alexandri de Loriol, 1876
                      Echinolampas chuni (Döderlein, 1905)
                      Echinolampas crassa (Bell, 1880)
                      Echinolampas depressa Gray, 1851
                      Echinolampas keiensis (Mortensen, 1948)
                      Echinolampas koreana H. L. Clark, 1925
                      Echinolampas rangii Desmoulins, 1837
                      Echinolampas sternopetala A. Agassiz & H. L. Clark, 1907
                      Echinolampas sumatrana (Döderlein, 1905)
                    Genus *Conolampas* (A. Agassiz, 1883)
                      Conolampas sigsbei (Agassiz, 1878)
                      Conolampas diomedea Mortensen, 1948
                      Conolampas malayana Mortensen, 1948
                      Conolampas murrayana Mortensen, 1948
                  Family Cassidulidae L. Agassiz & Desor, 1847
                    Genus *Cassidulus* Lamarck, 1801
                      Cassidulus caribaearum Lamarck, 1801
                      Cassidulus infidus Mortensen, 1948
                      Cassidulus mitis Krau, 1954
                      Cassidulus malayanus (Mortensen, 1948)
                  Genus *Eurhodia* Haime in d'Archiac & Haime, 1853
                    Eurhodia relicta Mooi, 1990
                  Genus *Oligopodia* Duncan, 1889
                    Oligopodia epigonus (van Martens, 1865)

Genus *Rhyncholampas* A. Agassiz, 1869
  Rhyncholampas pacificus (A. Agassiz, 1863)
Genus *Studeria* Duncan, 1891
  Studeria recens (A. Agassiz, 1879)
Family Apatopygidae Kier, 1962
  Genus *Apatopygus* Hawkins, 1920
    Apatopygus recens (Milne Edwards, 1863)
    Apatopygus occidentalis H. L. Clark, 1938
  Genus *Porterpygus* Baker, 1983
    Porterpygus kieri Baker, 1983
Family Neolampadidae Lambert, 1918
  Genus *Neolampas* A. Agassiz, 1869
    Neolampas rostellata A. Agassiz, 1869
  Genus *Anochanus* Grube, 1868
    Anochanus sinensis Grube, 1868
  Genus *Aphanopora* de Meijere, 1902
    Aphanopora echinobrissoides de Meijere, 1902
  Genus *Nannolampas* Mortensen, 1948
    Nannolampas tenera (de Meijere, 1902)
  Genus *Tropholampas* H. L. Clark, 1923
    Tropholampas loveni (Studer, 1880)

Key to the Living Cassiduloids

The following key relies on morphology of the test and external appendages, particular aspects of which are illustrated in Figs. 1–5. The species themselves are illustrated at the end of the key, in Figs. 6–12 (see Annotated List). When a species is encountered within the key, an abbreviated description of its range is given in square brackets, followed by a statement of its known bathymetric range. Nomenclatural authorities and other taxonomic information can be found in the annotated list of species that follows the key. Anatomical terminology is that of Mooi (1989).

1. Petaloids strongly developed (Figs. 6–11); respiratory podia with well-developed inner and outer pores; phyllodes conspicuous; bourrelets moderately to strongly developed 2
– Petaloids completely absent (Fig. 12); when present, aboral podia are single-pored, and not developed into respiratory podia; phyllodes inconspicuous, usually lacking inner series of phyllopores; bourrelets poorly developed or lacking 26
2. Apical system monobasal, without separate genital plates (Fig. 1a); naked zone present medially on oral surface (except in *Studeria recens* [Fig. 10d]), although not always strongly developed (Figs. 6–10); anal sulcus absent, or typically (except in *Cassidulus malayanus* [Fig. 9c]) short and shallow (Figs. 6–10); buccal podia present; globiferous pedicellariae absent 3
– Apical system tetrabasal, with separate genital plates (Fig. 1b); naked zone absent (Fig. 11); anal sulcus long and very deep (Fig. 11); buccal podia absent; globiferous pedicellariae present 24
3. Periproct just submarginal (Figs. 6–8); anal sulcus absent; three large, triangular plates along adoral edge of periproctal membrane (Fig. 2a);

ophicephalous pedicellariae with distal, closed oval ring of gripping teeth (Fig. 3a); many calcite spicules in stem of non-respiratory podia 4

– Periproct aboral or marginal (Figs. 9, 10); anal sulcus present, often weakly developed; more than four or five large plates in adoral part of periproctal membrane (Fig. 2b); ophicephalous pedicellariae with distal, U-shaped row of distal teeth (Fig. 3b); no spicules in stem of non-respiratory podia, but some spicules may occur in sucker tip of podium 17

4. Test margin oval in outline with periproct on slight posterior projection, or rostrum (Figs. 6, 7); oral surface concave (Figs. 6, 7); peristome slightly displaced anteriorly; primary aboral spination relatively dense, average distance between spine tubercles less than 1.5 times primary spine tubercle diameter (*Echinolampas*) 5

– Test margin almost circular in outline, rostrum very short, or absent (Fig. 8); oral surface flat (Fig. 8); peristome central, or slightly displaced posteriorly; primary aboral spination relatively sparse, average distance between spine tubercles more than twice primary spine tubercle diameter (*Conolampas*) . 14

5. Columns of respiratory podia in each petaloid very unequal in length, shorter column less than 60% length of longer in petaloid of ambulacra I and V (Figs. 6e, 7a, b, d) 6

– Columns of respiratory podia in each petaloid not very unequal in length, shorter column more than 65% length of longer in petaloid of ambulacra I and V (Figs. 6a–d, 7c, e) 9

6. Peristome oval, bourrelets not projecting into peristome; peristome width more than 17% test width 7

– Peristome pentagonal, bourrelets slightly projecting into peristome; peristome width less than 15% test width 8

7. Test width greater than 85% test length; ambitus broadly rounded in cross section; oral surface tumid [northeastern Central America, Yucatan, southeastern U.S., Greater and Lesser Antilles to northeastern South America; 30–310 m] ....
.....*Echinolampas depressa* (Fig. 6e)

– Test width less than 85% test length; ambitus relatively sharp in cross section; oral surface somewhat flattened [Japan; 150–500 m] . *Echinolampas sternopetala* (Fig. 7d)

8. Apical system more than 40% test length away from anterior edge of test; test almost conical; ambitus relatively sharp in cross section; oral surface flattened [Kepulauan Kai, southern Philippines; 245–400 m] ....
..... *Echinolampas keiensis* (Fig. 7a)

– Apical system less than 35% test length away from anterior edge of test; test smoothly arched in side view; ambitus broadly rounded in cross section; oral surface tumid [Korean Strait; 73 m] ....
.....*Echinolampas koreana* (Fig. 7b)

9. Petaloids wide, eight or more primary spine tubercles in row across interporiferous zone half-way down petaloid of ambulacrum V; peristome pentagonal, bourrelets slightly projecting into peristome 10

– Petaloids narrow, fewer than eight primary spine tubercles in row across interporiferous zone half-way down petaloid of ambulacrum V; peristome oval, bourrelets not projecting into peristome 12

10. Test smoothly arched antero-pos-teriorly; ambitus broadly rounded in cross section; oral surface tumid; tuberculation of aboral surface fine, more than 100 primary spine tubercles in 25 mm²; outer pore of each respiratory podial pore pair circular or subcircular [Red Sea, northern Indian Ocean to western Australia; 9–75 m] . . . . *Echinolampas ovata* (Fig. 6a)
   - Test with relatively sharp ambitus; oral surface somewhat flattened; tuberculation of aboral surface coarse, fewer than 100 primary spine tubercules in 25 mm²; outer pore of each respiratory podial pore pair strongly elongate 11
11. Test high, height greater than 50% test length; tuberculation of aboral surface very coarse, fewer than 50 primary spine tubercules in 25 mm² [South Africa; 25–500 m] . . . . *Echinolampas crassa* (Fig. 6d)
   - Test low, height less than 50% test length; tuberculation of aboral surface not very coarse, more than 70 primary spine tubercles in 25 mm² [west coast of Africa, Cape Verde Islands; shallow to 1670 m] . . . . *Echinolampas rangii* (Fig. 7c)
12. Apical system almost central, more than 45% test length from anterior edge of test; width of periproct less than 15% test width; more than five primary spine tubercles in row across interporiferous zone half-way down petaloid of ambulacrum V [Sumatra; 371 m] . . . . *Echinolampas sumatrana* (Fig. 7e)
   - Apical system slightly anterior, less than 45% test length from anterior edge of test; width of periproct more than 16% test width; five or fewer primary spine tubercles in row across interporiferous zone half-way down petaloid of ambu-lacrum V 13

13. Test relatively wide, width greater than 85% test length; phyllodes widened, interrupting taper of ambulacra as they approach peristome [Red Sea, Indian Ocean, Malaysia; 8–365 m] . . . . *Echinolampas alexandri* (Fig. 6b)
   - Test relatively narrow, width less than 85% test length; phyllodes narrow, ambulacra tapering smoothly as they approach peristome [Sumatra; 371 m] . . . . *Echinolampas chuni* (Fig. 6c)
14. Spine tubercles on oral surface sparsely distributed, fewer than seven in 25 mm² in interambula-crum 5 next to peristome; outer pore of each respiratory pore pair round [West Indies; 120–800 m] . . . . *Conolampas sigsbei* (Fig. 8a)
   - Spine tubercles on oral surface relatively densely distributed, 10 or more in 25 mm² in interambula-crum 5 next to peristome; outer pore of each respiratory pore pair elongate 15
15. Peristome approximately central; periproct approximately half its own length away from ambitus; interporiferous zone of petaloids relatively wide, more than twice as wide as single column of respiratory podia as measured at a point half-way down anterior petaloid [Maldives; 230 m] . . . . *Conolampas murrayana* (Fig. 8d)
   - Peristome slightly posterior; periproct almost as far from ambitus as it is long; interporiferous zone of petaloids relatively narrow, less than twice as wide as a single column of respiratory podia as measured at a point half-way down anterior petaloid 16
16. Longest column of respiratory podia in each petaloid reaches ambitus when viewed from above

[Philippines; 265 m] . . . .
. . . . *Conolampas diomedeae* (Fig. 8b)
− Longest column of respiratory po-
dia in each petaloid ends well short
of ambitus when viewed from
above [eastern Indonesia, south-
ern Philippines; 245–400 m] . . . .
. . . . . *Conolampas malayana* (Fig. 8c)
17. Peristome longer than wide   18
− Peristome circular, or wider than
long   19
18. Periproct slightly longer than wide
[Indian Ocean, Malaysia; 35–140
m] . . . *Oligopodia epigonus* (Fig. 10b)
− Periproct wider than long [north-
ern South America; 57–112 m]   .
. . . . *Eurhodia relicta* (Fig. 10a)
19. Naked zone absent from medial
area of oral surface; three gono-
pores; columns of respiratory po-
dia in each petaloid equal in length
[Arafura Sea; 236 m] . . . .
. . . . *Studeria recens* (Fig. 10d)
− Large naked zone in medial area
of oral surface; four gonopores;
columns of respiratory podia in
each petaloid unequal in length,
with columns Ia, IIb, IIIb, IVa, and
Vb the shortest of each pair   20
20. Large forms, test of adults over 40
mm in length; more than 70 res-
piratory podia in anterior petaloid
of adults; more than 20 podial
pores in anterior phyllode [Gulf of
California to west coast of Pana-
ma, Galapagos; 2–130 m] . . . . . .
. . *Rhyncholampas pacificus* (Fig. 10c)
− Relatively small forms, test of
adults less than 30 mm in length;
fewer than 60 pore pairs in anterior
petaloid of adults; fewer than 15
podial pores in anterior phyllode
(*Cassidulus*)   21
21. Periproct longer than wide, located
aborally, about half the distance
from the apical system to the pos-
terior edge; anal sulcus long, nar-
row, without conspicuous hood

over periproct [Indonesia; 250–290
m] . . . *Cassidulus malayanus* (Fig. 9c)
− Periproct round, or wider than
long, located aborally, consider-
ably more than half the distance
from the apical system to the pos-
terior edge; anal sulcus short, wide,
with small but distinct hood over
periproct   22
22. Test height greater than 50% test
length; periproct subcircular; few-
er than 45 respiratory podia in an-
terior petaloid of adults [East coast
of South America?; shallow water,
precise locality and depth data un-
available] *Cassidulus infidus* (Fig. 9b)
− Test height less than 50% test
length; periproct distinctly wider
than long; more than 45 respira-
tory podia in anterior petaloid of
adults   23
23. Apical system less than 40% test
length from anterior edge; test rel-
atively wide, more than 80% test
length [Belize, Bahamas to Bar-
bados; very shallow, 2–10 m] . . .
. . . . *Cassidulus caribaearum* (Fig. 9a)
− Apical system approximately 40%
test length from anterior edge; test
relatively narrow, less than 80%
test length [Sepetiba Bay, Brazil;
shallow water, precise depth data
unavailable] . . . .
. . . . *Cassidulus mitis* (Fig. 9d)
24. Three gonopores; petaloids slight-
ly reduced, fewer than 16 pore pairs
in ambulacrum III of large adults;
peristome roughly pentagonal
[Three Kings Islands, New Zea-
land; 90–300 m] . . . .
. . . . *Porterpygus kieri* (Fig. 11c)
− Four gonopores; at least 17 pore
pairs in ambulacrum III of large
adults; peristome transversely oval,
or roughly triangular (*Apatopygus*)
. . . .   25
25. Test large, adults commonly
reaching 40 mm in length; more

than 20 hydropores in madreporic plate; valves of globiferous pedicellariae with short blade and a single pair of long, distal, fang-like teeth (Fig. 4a) [New Zealand; 5–145 m] . *Apatopygus recens* (Fig. 11a)
–   Test small, adults usually less than 20 mm in length; fewer than 15 hydropores in madreporic plate; valves of globiferous pedicellariae with long, narrow blade and two pairs of long, distal, fang-like teeth (Fig. 4b) [southern and southwestern Australia; 17–40 m] . . . .
   . . . *Apatopygus occidentalis* (Fig. 11b)
26. Periproct on ambitus, or slightly submarginal, not in deep anal sulcus   27
–   Periproct aboral, in deep anal sulcus   29
27. Apical system sunken to form aboral "marsupium" in females; podial pores entirely absent from aboral ambulacra; four gonopores [South Africa; 135–350 m] . . . . .
   . . . . . . *Tropholampas loveni* (Fig. 12e)
–   Apical system not sunken in females; podial pores present in aboral ambulacra; two or three gonopores (four in rare individuals) . .   28
28. Apical system monobasal, without separate genital plates; typically three gonopores (rarely four, never two); valves of ophicephalous pedicellariae lacking thorns on proximal "handle" (Fig. 5a) [West Indies, Mediterranean; 145–1260 m]
   . . . . . *Neolampas rostellata* (Fig. 12a)
–   Apical system tetrabasal, with separate genital plates; two gonopores; valves of ophicephalous pedicellariae with prominent thorns on proximal part of "handle" on largest valve (Fig. 5b) [East Indies, Timor Sea; 390 m] . . . . . .
   . . . . . *Nannolampas tenera* (Fig. 12d)
29. Apical system sunken to form aboral "marsupium" [China Sea;

depth unknown] . . . .
   . . . . *Anochanus sinensis* (Fig. 12b)
–   Apical system not sunken [East Indies, northern and northeastern Australia; 350–710 m] . . . .
   . . . . *Aphanopora echinobrissoides*
                                        (Fig. 12c)

Annotated List of Cassiduloid Genera and Species

This list of genera is arranged by family according to Kier & Lawson (1978), which is in turn largely based on Kier (1962). I depart from their arrangement only in not recognizing the family Pliolampadidae Kier, 1962, pending phylogenetic revision of that group to resolve systematic problems that Kier (1962) himself acknowledged. As a result, *Eurhodia* (which Kier placed in the Pliolampadidae) is here placed in the Cassidulidae, following Mooi (1990). *Studeria* is also provisionally recognized as a cassidulid. *Oligopodia,* which Kier & Lawson (1978:125) listed among the "doubtful nominal genera," is here considered to be a cassidulid as well, as its similarity to some members of the genus *Eurhodia* suggests. Species described after 1948 are placed in the genera and families to which they were assigned by the original authors. Generic synonymies can be found in Kier (1962), and complete species descriptions and synonymies in Mortensen (1948), Krau (1954), Baker (1983), and Mooi (1990). The type species for each genus is indicated by an asterisk (*). Within families, genera are listed alphabetically after the type genus, and species are listed alphabetically within genera. Illustrations of these taxa (Figs. 6–12) follow this same arrangement.

Order Cassiduloida Claus, 1880
Family Echinolampadidae Gray, 1851
Echinolampas Gray, 1825
Echinolampas ovata (Leske, 1778)*
Fig. 6a

Geographic range. — A widespread species occurring in the Red Sea and the tropical
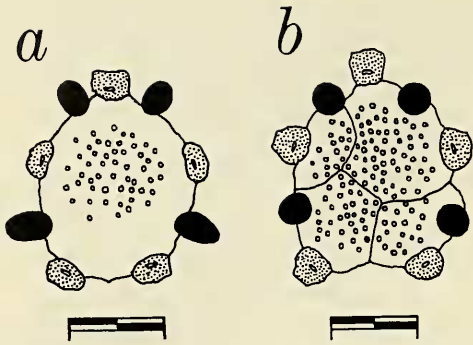
Fig. 1. Apical systems of cassiduloids: a, Monobasal system of *Cassidulus caribaearum* Lamarck, 1801 [Anegada, British Virgin Islands]; b, Tetrabasal system of *Apatopygus recens* (Milne Edwards, 1863) [USNM E16325]. Hydropores represented by open circles, gonopores in solid black, ocular plates shaded, genital plates unshaded, anterior towards top of page. Scale bar is 1 mm long.
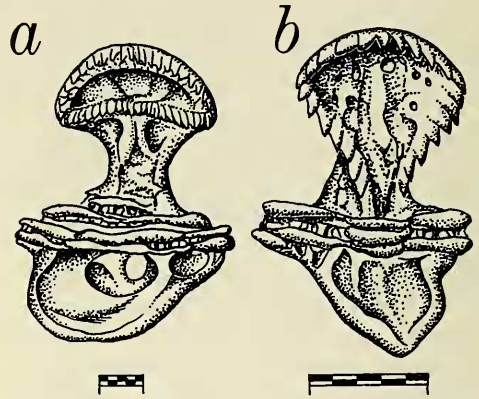

Fig. 3. Valves from ophicephalous pedicellariae of echinolampadids and cassidulids: a, *Conolampas sigsbei* (A. Agassiz, 1878) [USNM E12941] showing closed oval of distal teeth; b, *Cassidulus caribaearum* Lamarck, 1801 [Anegada, British Virgin Islands] showing U-shaped, open row of distal teeth. Scale bars are 50 μm long.

Indian Ocean eastward to the northwestern coast of Australia.

Bathymetric range.—9 to 75 m (Mortensen 1948).

Remarks.—Several attempts have been made to subdivide the genus *Echinolampas* into separate genera and subgenera (Mortensen 1948). None of these schemes have become universally accepted, and Kier (1962:107) finally decided "that all these sections and subgenera are based on characters too variable to be of generic distinc-

Fig. 2. Periproctal plate patterns of echinolampadids and cassidulids: a, *Echinolampas depressa* Gray, 1851 [USNM E12929]; b, *Cassidulus caribaearum* Lamarck, 1801 [Anegada, British Virgin Islands]. Periproct in solid black, primary spine tubercles represented by two concentric circles, miliary spine tubercles by single open circle, aboral is towards top of page. Scale bars are 1 mm long.

tion." In spite of Kier's (1962) attempt to revive the name *Echinolampas oviformis* (Gmelin, 1789) for *Echinolampas ovata,* recent authors (Clark & Rowe 1971, Dollfus & Roman 1981) have argued convincingly for the retention of Leske's (1778) old name. This species apparently can be found in the littoral zone of the Red Sea (Dollfus & Roman 1981). This is supported by observations of this species in the intertidal, on fine carbonate sand without mud at Ashmore Reef, N. W. Australia (Lyle Vail, pers. comm.). At this locality, *E. ovata* also appears to have a diurnal activity cycle, "burrowing through the sand with about half of their test exposed" at night, but remaining more deeply burrowed during the day (Lyle Vail, pers. comm.). McNamara & Philip (1980) speculated that this species lives slightly inclined, with the posterior deeper in the substrate, buried in the sand up to the level of the petaloids.

Echinolampas alexandri de Loriol, 1876
Fig. 6b

Geographic range.—The Red Sea and throughout the Indian Ocean and Malaysia.
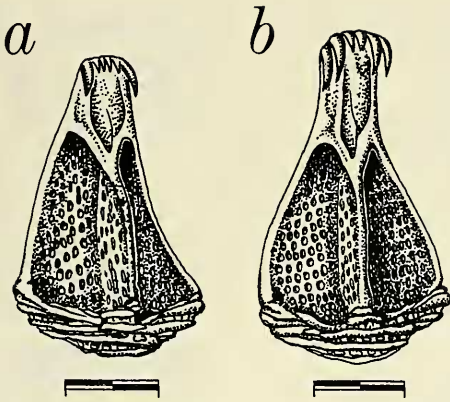
Fig. 4. Valves from globiferous pedicellariae of apatopygids: a, *Apatopygus recens* (Milne Edwards, 1863) [USNM E11089] showing single pair of fanglike teeth; b, *Apatopygus occidentalis* H. L. Clark, 1938 [after Baker 1983] showing two pairs of fang-like teeth. Scale bars are 100 μm long.
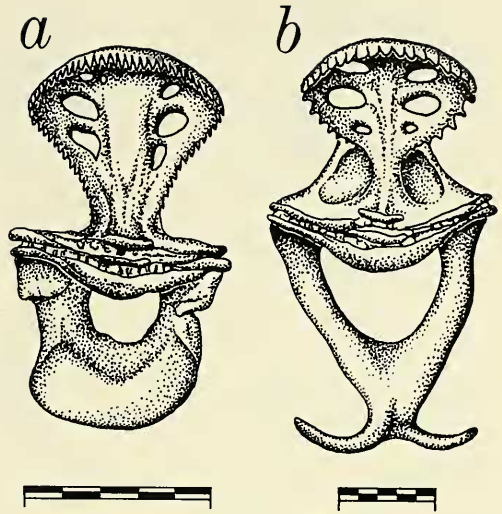

Fig. 5. Valves from ophicephalous pedicellariae of neolampadids: a, *Neolampas rostellata* A. Agassiz, 1869 [USNM E20529], illustrating absence of thorns on "handle"; b, *Nannolampas tenera* (de Meijere, 1902) [after Mortensen 1948] showing presence of thorns on "handle." Scale bars are 50 μm long.

Bathymetric range. — 8 to 365 m.

Remarks. — Mortensen (1948) reported two subspecies (*E. alexandri sibogae* and *E. alexandri forcipulata*) to which Dollfus & Roman (1981) added a third (*E. alexandri arctambulacrum*). Mortensen (1948) felt that *E. ovata* and *E. alexandri* were very distinct, but because of variation in both species, Dollfus & Roman (1981) suggested that there is considerable overlap in morphology. Although more material from all parts of their ranges will be necessary before a complete comparison can be made, based on differences in petaloid width and peristome shape (see key, above), it would appear that *E. ovata* and *E. alexandri* are good species.

Echinolampas chuni (Döderlein, 1905)
Fig. 6c

Geographic range. — Known only from two denuded specimens from Sumatra (Döderlein 1906).

Bathymetric range. — From a single "Valdivia" station at 371 m.

Remarks. — No new information has come to light since Döderlein's (1906) and Mortensen's (1948) descriptions. Since the only known specimens were dead when collected, nothing is known of the biology of this species.

Echinolampas crassa (Bell, 1880)
Fig. 6d

Geographic range. — Known only from the South African coast.

Bathymetric range. — Mortensen (1948) says 25 to 500 m, but Thum & Allen (1975) record it from as shallow as 12 m.

Remarks. — The ecology of this species is amongst the best known of all cassiduloids. Thum and Allen (1975:362) reported that this echinoid prefers the ripple slopes of ripple beds composed of biogenic substrates (75–95% calcium carbonate), and that it is "an indirect deposit feeder and habitually burrows during feeding," being frequently overlain by 30 to 50 mm of substrate. They also estimated a growth rate of approximately 5 mm of test length per year. Their largest specimen was about 125 mm in length, suggesting (p. 373) "that this lamp urchin must be rather long-lived." Thum &
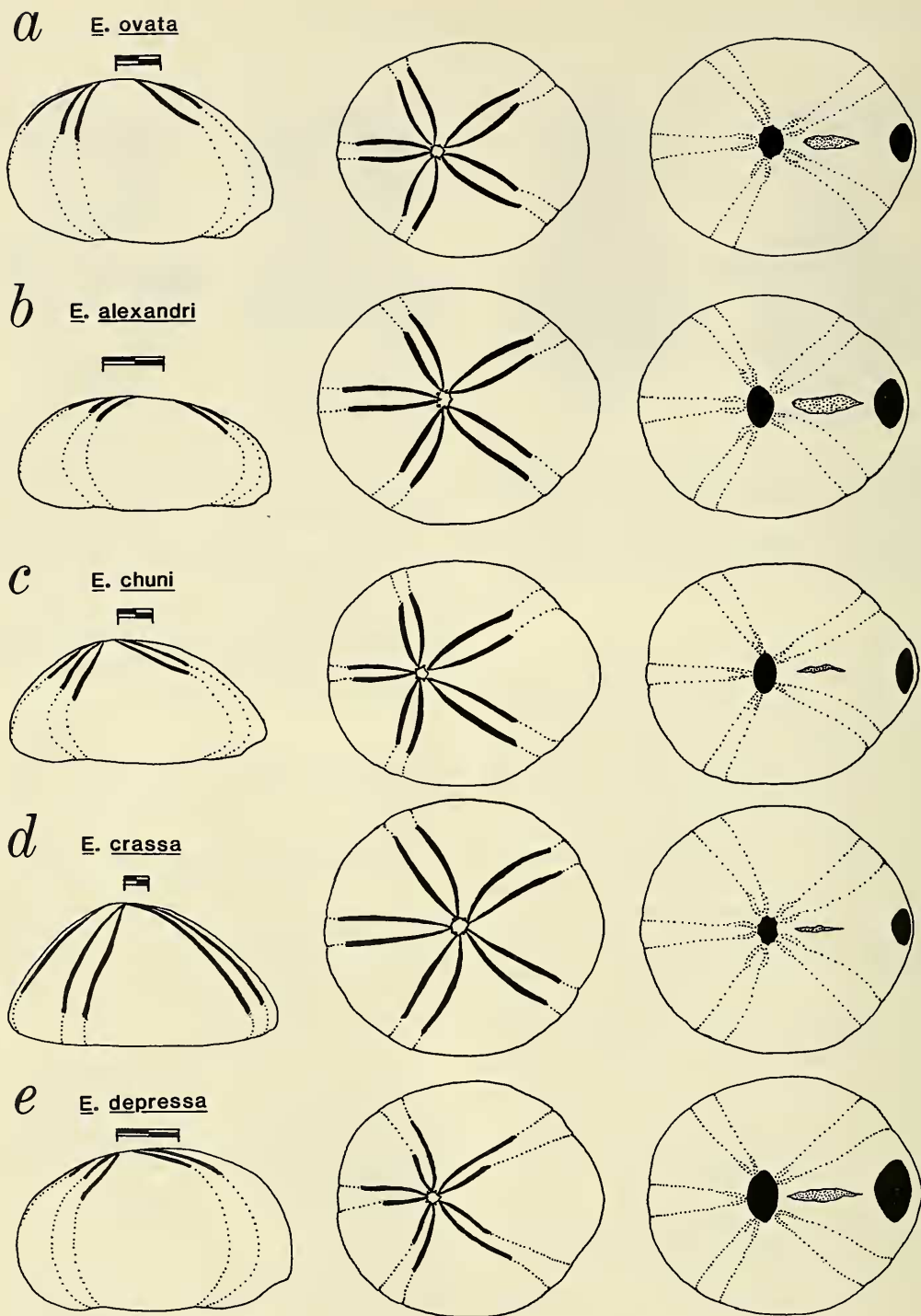
Fig. 6.   Family Echinolampadidae, genus *Echinolampas*: a, *E. ovata* (Leske, 1778) [after Mortensen 1948]; b, *E. alexandri* de Loriol, 1876 [after Mortensen 1948]; c, *E. chuni* (Döderlein, 1905) [after Döderlein 1906]; d, *E. crassa* (Bell, 1880) [after Mortensen 1948]; e, *E. depressa* Gray, 1851 [Florida Department of Natural Resources I3562]. From left to right for each species: lateral view, aboral view, oral view. Anterior end is to the left. Petaloids, peristomes, and periprocts in solid black, naked zone stippled. All scale bars are 10 mm long.

72
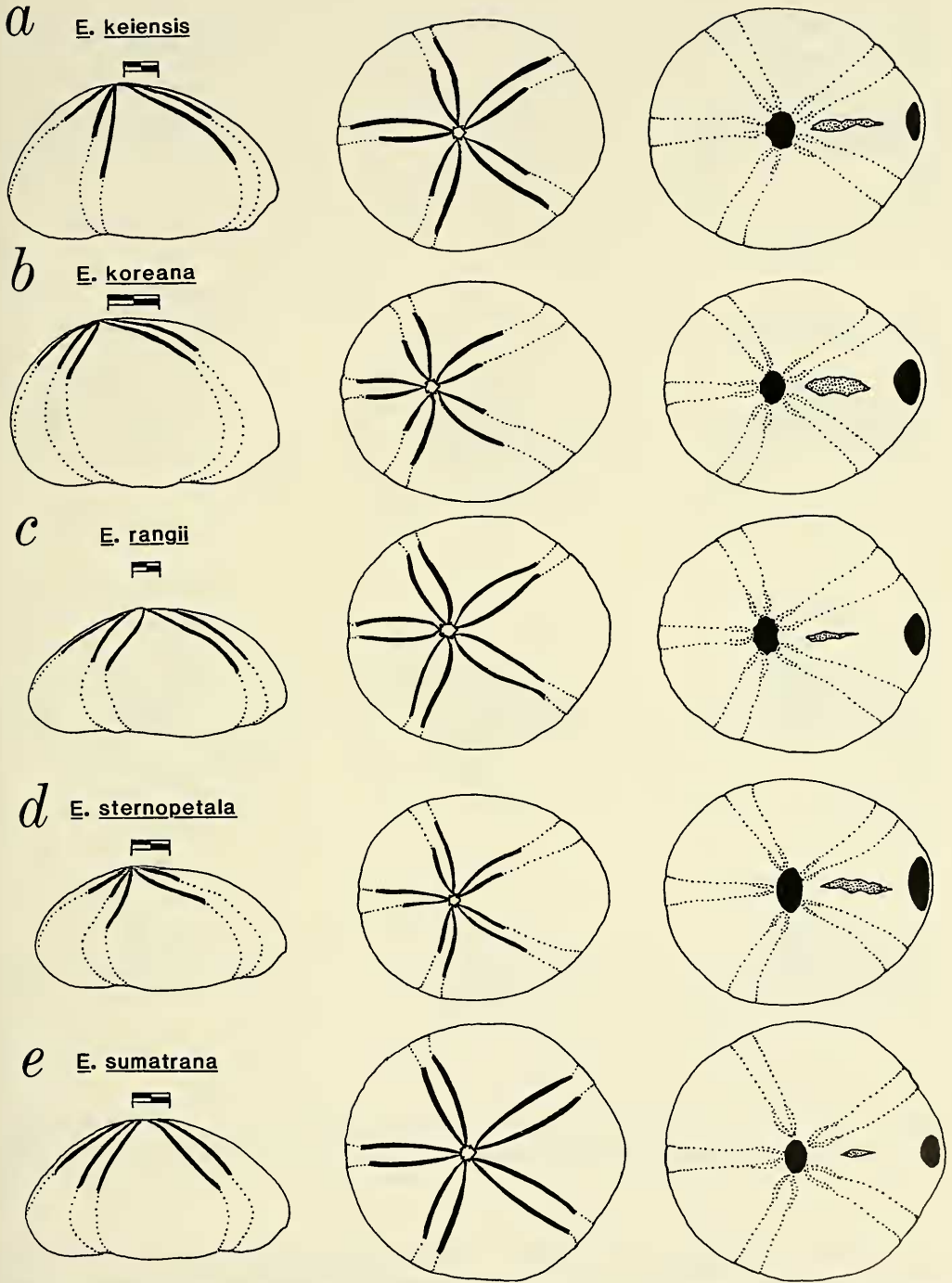
Fig. 7.   Family Echinolampadidae, genus *Echinolampas* (cont'd): a, *E. keiensis* (Mortensen, 1948) [after Mortensen 1948]; b, *E. koreana* H. L. Clark, 1925 [after Clark 1925 and Mortensen 1948]; c, *E. rangii* Desmoulins, 1837 [after Agassiz 1872]; d, *E. sternopetala* A. Agassiz & H. L. Clark, 1907 [after Mortensen 1948]; e, *E. sumatrana* (Döderlein, 1905) [after Döderlein 1906]. Conventions as in Fig. 6. All scale bars are 10 mm long.
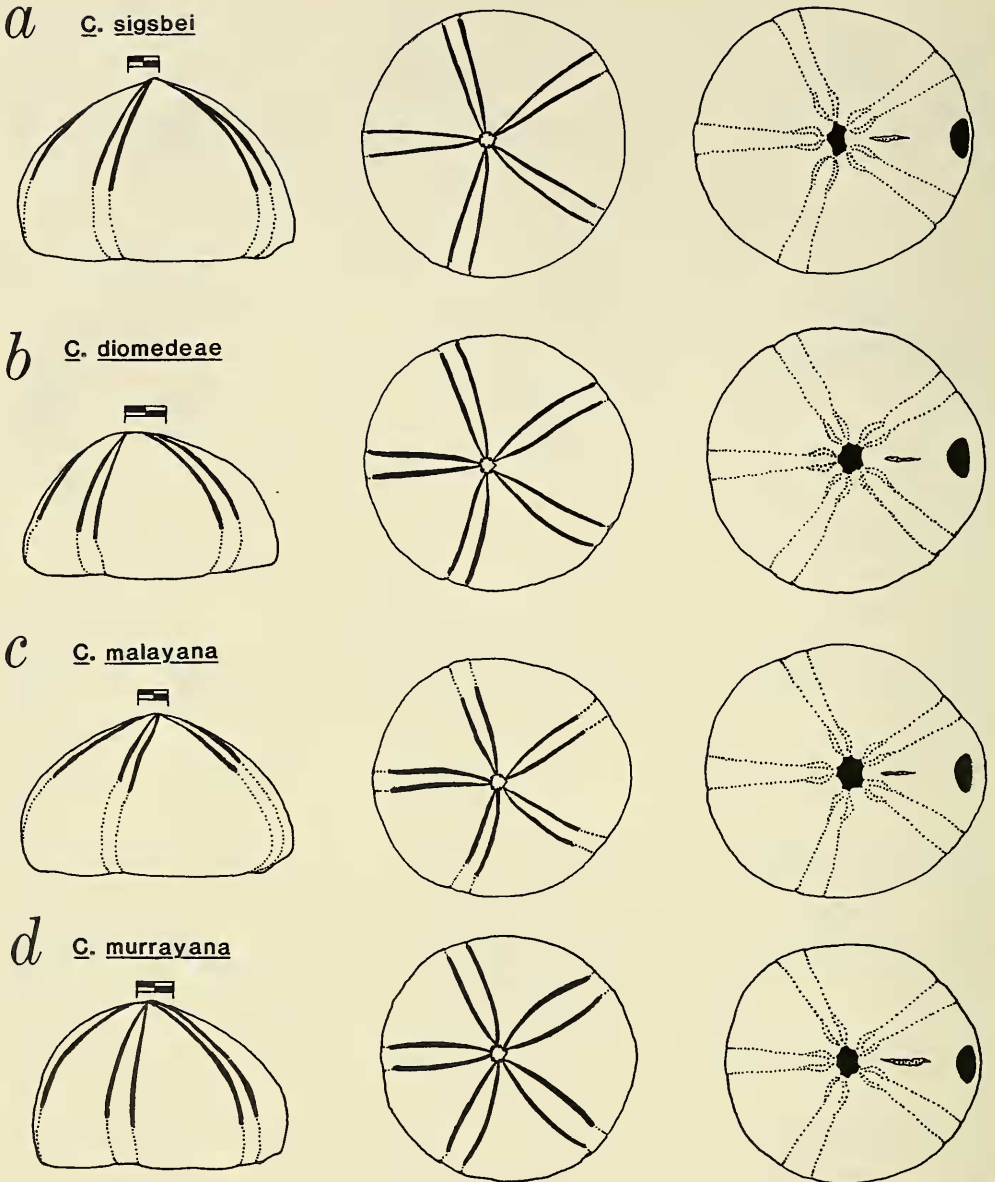
Fig. 8. Family Echinolampadidae (cont'd), genus *Conolampas*: a, *C. sigsbei* (A. Agassiz, 1878) [after Kier 1962]; b, *C. diomedeae* Mortensen, 1948 [after Mortensen 1948]; c, *C. malayana* Mortensen, 1948 [after Mortensen 1948]; d, *C. murrayana* Mortensen, 1948 [after Mortensen 1948]. Conventions as in Fig. 6. All scale bars are 10 mm long.

Allen (1976:27) later analyzed the breeding behavior of *E. crassa,* discovering a "remarkable synchrony of gonad tissue mass both within and between sexes." They also compared ambient substrate and gut content particle dimensions, and suggested that larger particles are excluded from the diet because of the fixed mouth size, and smaller ones because the animal has difficulty manipulating them (Thum & Allen 1976). These echinoids feed using the oral podia to lift particles to the peristome and can also
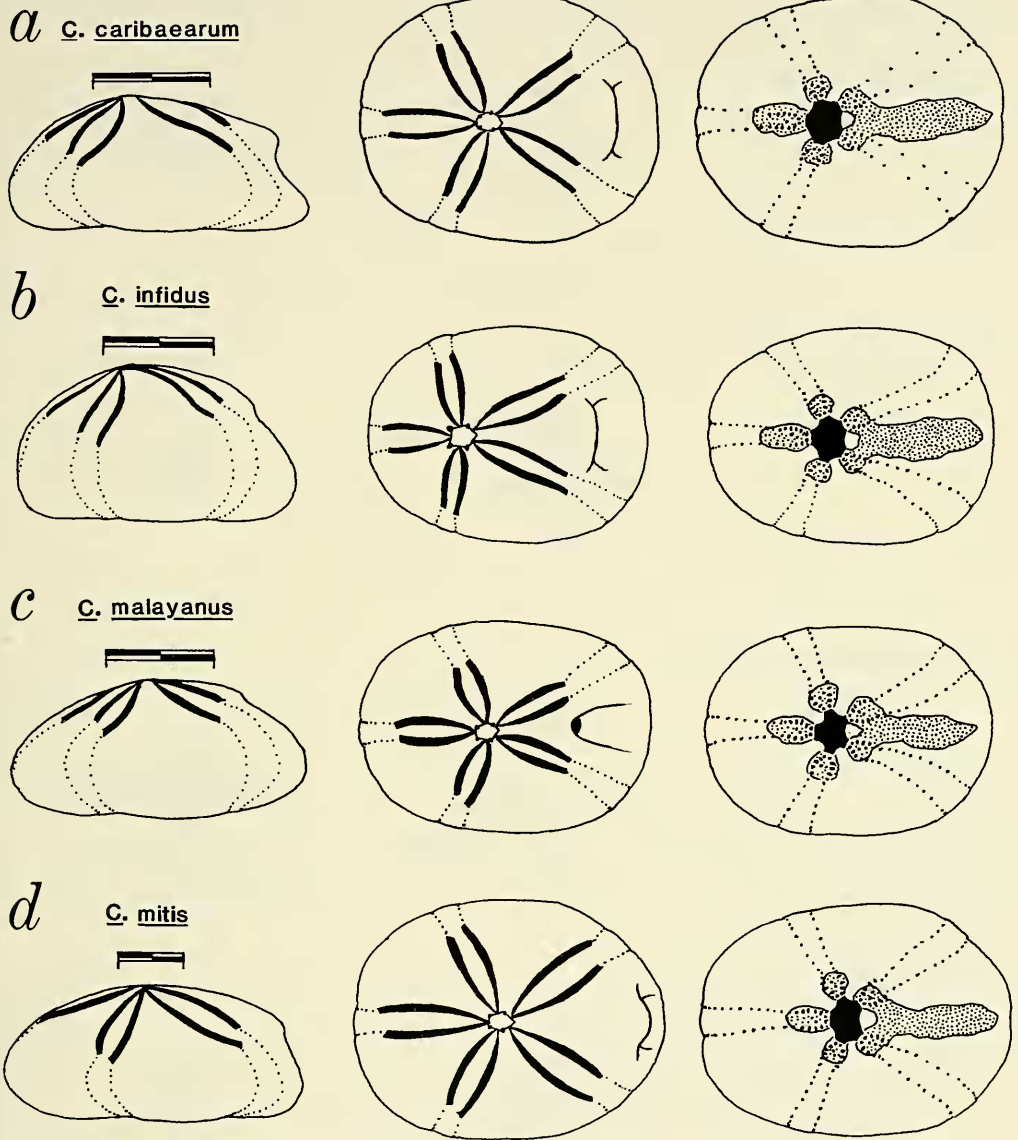
Fig. 9.   Cassidulidae, genus *Cassidulus*: a, *C. caribaearum* Lamarck, 1801 [Anegada, British Virgin Islands]; b, *C. infidus* Mortensen, 1948 [after Mortensen 1948]; c, *C. mitis* Krau, 1954 [after Krau 1954]; d, *C. malayanus* (Mortensen, 1948) [after Mortensen 1948]. Conventions as in Fig. 6. All scale bars are 10 mm long.

use the circum-oral bourrelet spines to elevate particles into the mouth (Thum & Allen 1976). Cram (1971) described the early life history and larval morphology of *E. crassa,* reporting that metamorphosis occurred at about 40 days after fertilization.

Echinolampas depressa Gray, 1851
Figs. 2a, 6e

Geographic range.—From eastern Central America as far north as the north coast of the Yucatan, the southeastern U.S., both coasts of Florida, the Greater and Lesser
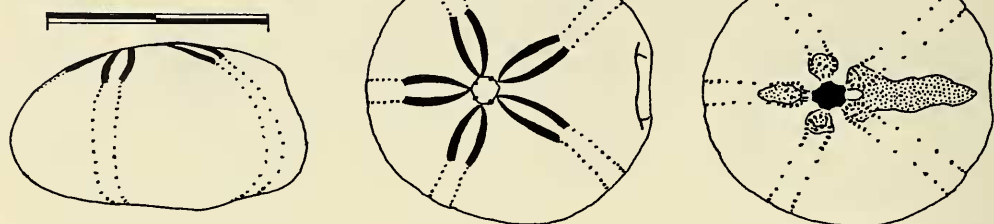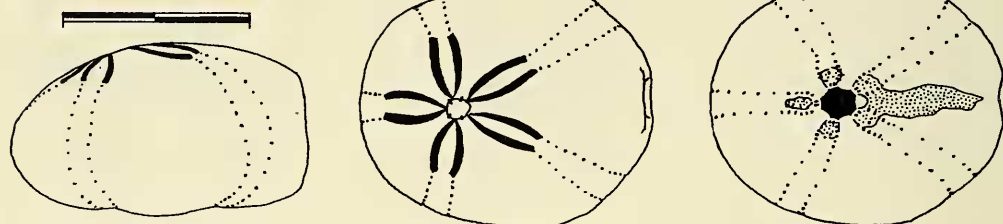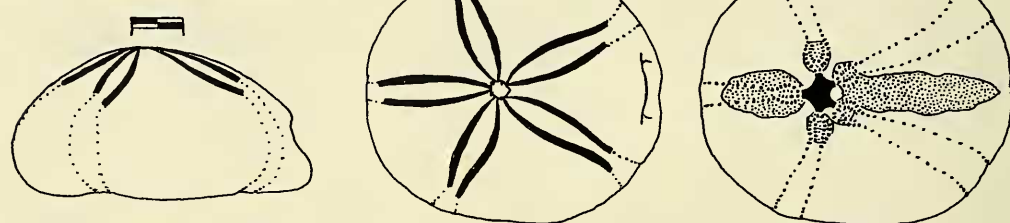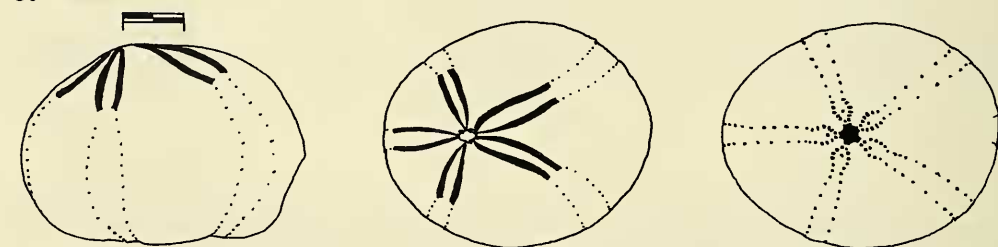
Fig. 10. Cassidulidae (cont'd): a, *Eurhodia relicta* Mooi, 1990 [Holotype, USNM E20480]; b, male *Oligopodia epigonus* (van Martens, 1865) [USNM E35684]; c, *Rhyncholampas pacificus* (A. Agassiz, 1863) [after Kier 1962]; d, *Studeria recens* (A. Agassiz, 1879) [after Agassiz 1881]. Conventions as in Fig. 6. All scale bars are 10 mm long.

Antilles south to northeastern South America as far east as French Guyana.

Bathymetric range.—30 to 310 m (Serafy 1979).

Remarks.—Märkel (1978) described the Aristotle's lantern from juveniles of this species. The lantern disappears as the animal approaches 5 mm in length and does

a, Apatopygus recens
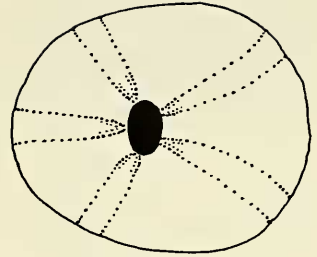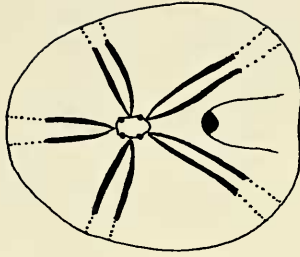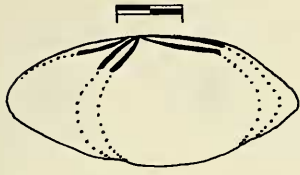
b, Apatopygus occidentalis
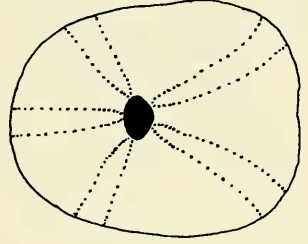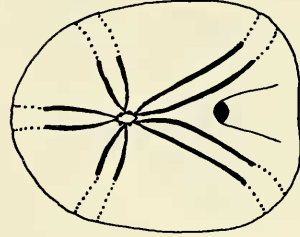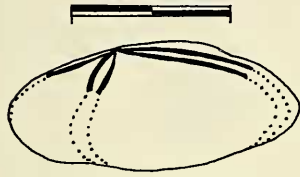
c, Porterpygus kieri
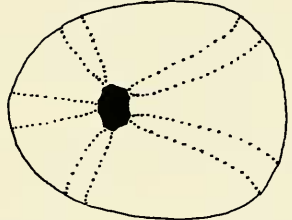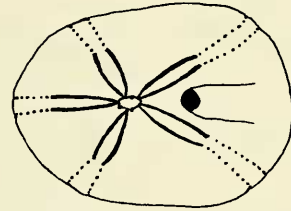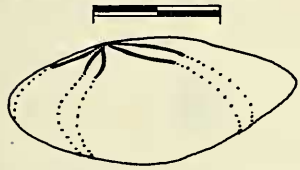
Fig. 11. Apatopygidae: a, *Apatopygus recens* (Milne Edwards, 1863) [USNM E16325]; b, *Apatopygus occidentalis* H. L. Clark, 1938 [after Baker 1983]; c, *Porterpygus kieri* Baker, 1983 [after Baker 1983]. Conventions as in Fig. 6. All scale bars are 10 mm long.

not appear to function at all in the feeding of the echinoid. Serafy (1979) documented the occurrence of this species in the Gulf of Mexico on carbonate sands consisting largely of calcareous algal fragments. In spite of the apparent frequency with which this species is collected, little else is known of its ecology.

Echinolampas keiensis (Mortensen, 1948)
Fig. 7a

Geographic range.—Known only from Kepulauan Kai (Kei Islands) and from off Zamboanga in the southern Philippines (Mortensen 1948).

*Bathymetric range.*—245 to 400 m (Mortensen 1948).

Remarks.—This species has apparently not been encountered since Mortensen's (1948) original description. *E. keiensis* was originally placed in a separate genus, *Planilampas* Mortensen, 1948 along with *Echinolampas sternopetala* (see below).

Echinolampas koreana H. L. Clark, 1925
Fig. 7b

Geographic range.—From the Korean Strait (Clark 1925) and western Japan (Nisiyama 1968).

Bathymetric range.—73 to 100 m.

Remarks.—Clark (1925) compared his new species with *E. sternopetala*, and Nisiyama (1968) compared *E. koreana* with *E. alexandri. E. koreana* differs from both

a <u>Neolampas</u> <u>rostellata</u>

1.0
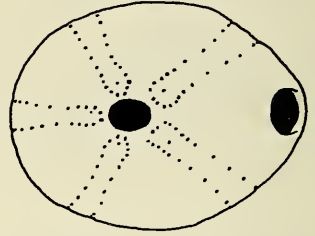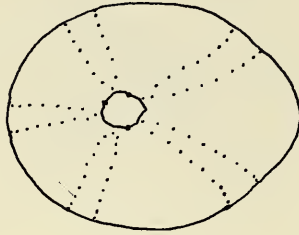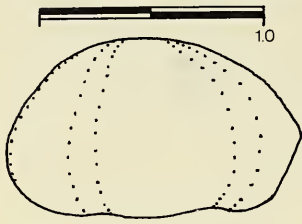
b <u>Anochanus</u> <u>sinensis</u>

0.5
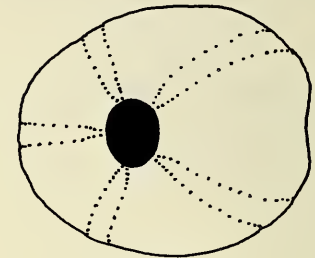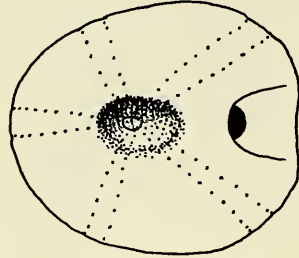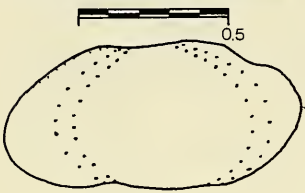
c <u>Aphanopora</u> <u>echinobrissoides</u>

0.5

d <u>Nannolampas</u> <u>tenera</u>

1.0

e <u>Tropholampas</u> <u>loveni</u>

0.5
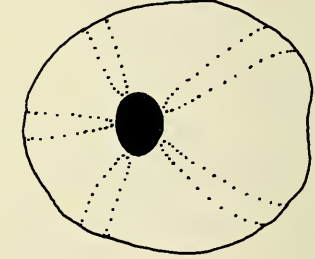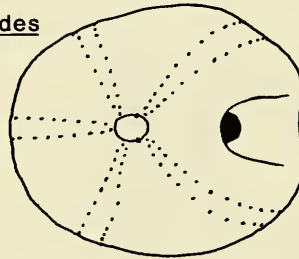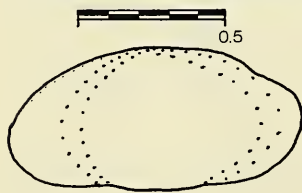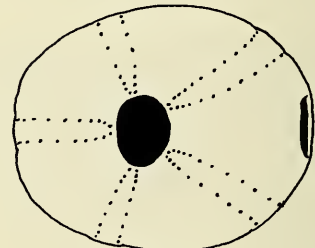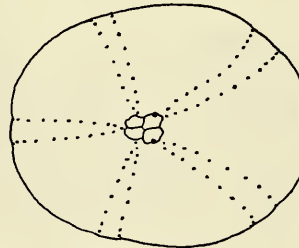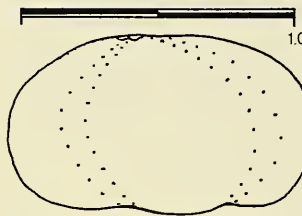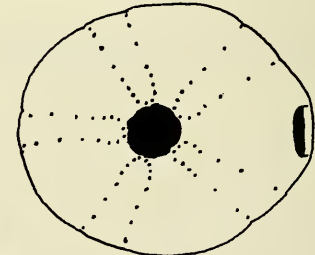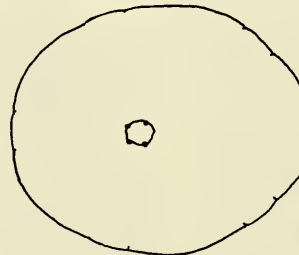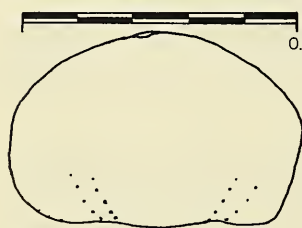
of the other species in having a much higher test and a pentagonal peristome. It also lacks the distinctive inequality in the length of the respiratory podial columns so strongly developed in the petaloids of *E. sternopetala*. For these reasons, I would agree with Mortensen (1948) in suggesting that these species are not particularly closely related. Nisiyama (1968) appears to be the only author to have published on *E. koreana* since Clark (1925) described it from a single specimen. Nothing has been published on the biology of this species.

Echinolampas rangii Desmoulins, 1837
Fig. 7c

Geographic range. — Apparently from the west coast of Africa (Senegal) and the Cape Verde Islands (Mortensen 1948).

Bathymetric range. — Mortensen (1948) recorded it from 1570 to 1670 m, but stated that it is undoubtedly also known from "shallow" water without suggesting an upper limit.

Remarks. — No work has been published on this species since Mortensen (1948).

Echinolampas sternopetala A. Agassiz & H. L. Clark, 1907
Fig. 7d

Geographic range. — Known only from Japanese waters from Sagami Bay to Kagoshima Bay (Shigei 1986).

Bathymetric range. — 100 to 500 m (Shigei 1986).

Remarks. — Mortensen (1948) made this the type species of a new genus, *Planilampas,* which he erected largely on the basis of the flatness of the oral surface. Kier (1962)

synonymized this genus with *Echinolampas*. Shigei (1986) described *Echinolampas sternopetala* from Sagami Bay, Japan, but provided no comments on substrate type or ecology.

Echinolampas sumatrana (Döderlein, 1905)
Fig. 7e

Geographic range. — Known from a single denuded test collected off Sumatra.

Bathymetric range. — From a single "Valdivia" station at 371 m.

Remarks. — Mortensen (1948) agreed with Döderlein (1906) in suggesting that more specimens of *E. sumatrana* were necessary before it could be firmly established that it was distinct from *E. crassa*. However, differences in peristome shape and petaloid width (see key, above) seem to indicate that *E. sumatrana* is distinct from *E. crassa*.

Conolampas (A. Agassiz, 1883)
Conolampas sigsbei (A. Agassiz, 1878)*
Figs. 3a, 8a

Geographic range. — Throughout the Greater and Lesser Antilles, west coast of Florida, and the north and northeastern coasts of the Yucatan.

Bathymetric range. — 120 to 800 m.

Remarks. — Mooi (1990) recently summarized what little is known of the biology of this species, suggesting that it lives on the surface of the sediment, not burrowed, and feeds on relatively fine carbonate substrates. Judging from the flatness of the oral surface and overall similarity in spination and test shape, other species of *Conolampas* probably have similar habits.

←

Fig. 12.   Neolampadidae: a, *Neolampas rostellata* A. Agassiz, 1869 [MCZ 2739]; b, presumed female *Anochanus sinensis* Grube, 1868 [reconstructed from Mortensen 1948 and McKnight 1968]; c, presumed male *Aphanopora echinobrissoides* de Meijere, 1902 [after McKnight 1968]; d, *Nannolampas tenera* (de Meijere, 1902) [after Mortensen 1948]; e, male *Tropholampas loveni* (Studer, 1880) [after Mortensen 1948 and MCZ 4507]. Conventions as in Fig. 6. All scale bars in mm.

Conolampas diomedeae Mortensen, 1948
Fig. 8b

Geographic range. — Mortensen (1948) recorded a single specimen (the holotype) from off Mindoro Island in the Philippines. David & de Ridder (1989) describe an additional seven specimens from the Philippines.

Bathymetric range. — Mortensen's (1948) specimen was dredged from 265 m, David and de Ridder's (1989) from stations between 181 and 195 m.

Remarks. — David & de Ridder's (1989) specimens are the only ones collected since Mortensen's (1948) description. They provide some biometrics and figures, but no information on the biology of this species.

Conolampas malayana Mortensen, 1948
Fig. 8c

Geographic range. — Known only from Kepulauan Kai (Kei Islands) and off Zamboanga in the southern Philippines (Mortensen 1948).

Bathymetric range. — 245 to 400 m.

Remarks. — No new information since Mortensen (1948) discovered the species.

Conolampas murrayana Mortensen, 1948
Fig. 8d

Geographic range. — Only two specimens known from off the Maldive Islands in the Indian Ocean.

Bathymetric range. — Dredged from 229 m.

Remarks. — No new information since Mortensen (1948).

Family Cassidulidae L. Agassiz &
Desor, 1847
Cassidulus Lamarck, 1801
Cassidulus caribaearum Lamarck, 1801*
Figs. 1a, 2b, 3b, 9a

Geographic range. — Belize, Central America, and from the Bahama Islands south through the Virgin, Leeward, and Windward Islands to Barbados.

Bathymetric range. — Very shallow water,

from less than 1 m to probably no deeper than 10 m. Agassiz (1872) reported fragments from 197 m, but it is not at all certain whether these actually represent *C. caribaearum.*

Remarks. — Some confusion has arisen on the spelling of the species name, recent papers reporting it as *C. cariboearum* (Kier 1975) and *C. caribbearum* (Gladfelter 1978). As Mortensen (1948) recorded, Lamarck's original and correct spelling is *C. caribaearum.* Kier (1975) described this species as living buried in coarse sand at Carrie Bow Cay, Belize. Gladfelter (1978) reported that *C. caribaearum* broods its young among the aboral spines and was locally abundant in coarse, oolitic carbonate sand in very shallow water. He also described locomotion in this species, which uses "ditaxic waves, passing from the front to the rear of large movable spines on the lateral portions of the ventral surface; this mechanism is unique among echinoids" (p. 149). *C. caribaearum* feeds in much the same way as described for *Echinolampas crassa* (see above), but apparently does not rely as much on activities of the circum-oral spination (Gladfelter 1978). Gladfelter (1978) also studied reproductive biology and seasonal variation in population density in this widely distributed, but surprisingly seldom encountered, shallow water cassiduloid.

Cassidulus infidus Mortensen, 1948
Fig. 9b

Geographic range. — Known only from a single specimen labeled "Bahia" (Mortensen 1948). Probably from the east coast of South America.

Bathymetric range. — No depth record exists for the holotype, but Mortensen (1948) felt that it probably occurs in shallow water.

Remarks. — Although Krau (1954) compared her new species, *C. mitis,* with *C. infidus,* she relied on Mortensen's (1948) description, as no new information has been published on the latter, poorly known species.

Cassidulus mitis Krau, 1954
Fig. 9c

Geographic range. — Known only from Sepetiba Bay, near Rio de Janeiro, Brazil.

Bathymetric range. — Krau (1954) did not provide precise depth data, but said that the new species was collected from "shallow waters."

Remarks. — Tommasi & Lima-Verde (1970) synonymized *Cassidulus delectus* Krau, 1960 with *C. mitis* and noted that *C. mitis* broods its young in a manner similar to that of *C. caribaearum* (Gladfelter 1978).

Cassidulus malayanus (Mortensen, 1948)
Fig. 9d

Geographic range. — Only two known specimens, both from Kepulauan Kai (Kei Islands), according to Mortensen (1948).

Bathymetric range. — Approximately 250–290 m (Mortensen 1948).

Remarks. — Mortensen (1948) described this species as a member of the genus *Procassidulus* Lambert, 1918. The latter genus was erected by Lambert (1918) to replace *Cassidulus,* which he thought was preoccupied (Mortensen 1948). Kier (1962) synonymized *Procassidulus* with *Rhynchopygus* d'Orbigny, 1856. *Rhynchopygus* is stated by Kier (1962) to have a tetrabasal apical system. According to Mortensen (1948), *Procassidulus malayanus* has a "compact" (=monobasal) apical system and so cannot be a *Rhynchopygus*. Since this species is so much like other species in *Cassidulus,* it appears best to place *C. malayanus* in this genus, at least until more material becomes available. Mortensen (1948:225) reported that the two specimens he studied were taken from a "sandy bottom."

Eurhodia Haime in d'Archiac & Haime, 1853
Eurhodia relicta Mooi, 1990
Fig. 10a

Geographic range. — Only two specimens known, the holotype from off western Suri-

nam, paratype from off Venezuela (Mooi 1990).

Bathymetric range. — Dredged from 57 and 112 m, respectively.

Remarks. — The type species of the genus is *Eurhodia morrisi* Haime in d'Archiac & Haime, 1853. *E. relicta* apparently occurs in terrigenous, siliceous substrates (Mooi 1990), but little else is known of its biology.

Oligopodia Duncan, 1889
Oligopodia epigonus (van Martens, 1865)*
Fig. 10b

Geographic range. — Mortensen (1948) recorded this species from off the east coast of Africa, the Malaysian region, off Jolo in the Philippines, and the Bonin Islands. Because specimens from off the northeast coast of Somalia, South Africa, Tonga, and New Zealand can be found in the U.S. National Museum (USNM), it would appear that this species ranges from the western Indian Ocean eastward through Indonesia and the Philippines all the way to the South Pacific Ocean. This means that *O. epigonus* has the largest range of any known living species of cassiduloid.

Bathymetric range. — Live specimens are recorded from 35 to 141 m. Mortensen reported dead specimens from 5 to 390 m, suggesting that the bathymetric range could be much greater than the live specimens indicate.

Remarks. — Females of this species have gonopores many times larger than those of the male (Mortensen 1948). Although once thought to be closely related to *Apatopygus,* *Oligopodia* differs in having a monobasal apical system and in ambulacral plate pattern and overall test shape. This genus appears to be much more closely related to *Eurhodia,* as noted by Mooi (1990). Mortensen (1948:232) said that "it is not rare in places with a suitable bottom, viz. a coarse sandy or even gravelly bottom" and reported that it occasionally is found in substrates with a high percentage of calcareous algal fragments.

Rhyncholampas A. Agassiz, 1869
Rhyncholampas pacificus
(A. Agassiz, 1863)*
Fig. 10c

Geographic range. — The tropical eastern Pacific Ocean, from the Gulf of California to the Gulf of Panama. Also known from the Galapagos Islands (Mortensen 1948).

Bathymetric range. — Clark (1925) said that it occurs from 7 to 130 m, but in his description of Rhyncholampas, Agassiz (1872) recorded it from water less than 2 m deep.

Remarks. — The biology of this large species of cassidulid is surprisingly poorly known. Agassiz (1872) mentioned that the living echinoid lives partially buried in the substrate up to the level of the petaloids, but no other direct observations of living specimens have since been reported.

Studeria Duncan, 1891
Studeria recens (A. Agassiz, 1879)
Fig. 10d

Geographic range. — Agassiz (1881) recorded the species from the Arafura Sea, south of Papua-New Guinea.

Bathymetric range. — Dredged from 236 m.

Remarks. — According to Kier (1962), the type species of the genus is Studeria elegans (Laube, 1869) because this was the only species included in the original description of the genus. Many previous authors had considered S. recens to be the type of Studeria. There is some uncertainty that S. recens is a Studeria, but there are strong similarities (except in overall test shape) between this species and Kier's (1962) figure of S. subcarinatus (Goldfuss, 1928). S. recens also fits the description of the genus (Kier 1962: 216), particularly with respect to the 3 gonopores, strongly developed bourrelets, and absence of an oral, medial naked zone. Kier (1962) synonymized Hypselolampas H. L. Clark, 1917 (which included H. recens) with Studeria because of a lack of significant characters separating S. recens from other

members of Studeria Duncan, 1891. No other occurrences of this poorly known species have been published since Agassiz's (1881) description and nothing is known of its biology apart from the fact that it was collected from mud.

Family Apatopygidae Kier, 1962
Apatopygus Hawkins, 1920
Apatopygus recens (Milne Edwards, 1863)*
Figs. 4a, 11a

Geographic range. — Known only from New Zealand.

Bathymetric range. — 6 to 146 m.

Remarks. — The behavior and general biology of this well-known species have been described by Higgins (1974). The echinoid burrows to a depth of approximately 30 mm into coarse sands or fine gravels composed of terrigenic material and high proportions of broken shell. Higgins (1974:513) suggested that A. recens is "an almost continuous deposit feeder," but did not describe the manner by which food is collected.

Apatopygus occidentalis
H. L. Clark, 1938
Figs. 4b, 11b

Geographic range. — Five specimens are known from along the western and southern coasts of Australia (Baker 1983).

Bathymetric range. — 17 to 40 m (Baker 1983).

Remarks. — Although Baker (1983) provided a detailed redescription of this very rare species, almost nothing is known of its general biology.

Porterpygus Baker, 1983
Porterpygus kieri Baker, 1983*
Fig. 11c

Geographic range. — Known only from five specimens collected near Three Kings Islands, New Zealand (Baker 1983).

Bathymetric range. —Dredged from approximately 90 to 300 m.

Remarks. —Baker (1983:172) suggested that the discovery of this second genus attributable to the family Apatopygidae "supports the isolation of Kier's Apatopygidae as a separate family." Nothing is known of the biology of this species.

Family Neolampadidae Lambert, 1918
Neolampas A. Agassiz, 1869
Neolampas rostellata A. Agassiz, 1869*
Figs. 5a, 12a

Geographic range. —West Indian waters and the Eastern Atlantic, particularly Florida, across the Atlantic to the Moroccan coast, and the Mediterranean.

Bathymetric range. —Mortensen (1948) reported the species from 145 to 1260 m.

Remarks. —Examination of specimens in the National Museum of Natural History (USNM) and the Museum of Comparative Zoology, Harvard (MCZ) reveals that, as in *Oligopodia,* females of this species have much larger gonopores than the males. Although this species is fairly well known from North American waters, its preference for deep waters has prevented direct observation of habits.

Anochanus Grube, 1868
Anochanus sinensis Grube, 1868*
Fig. 12b

Geographic range. —Reported only from the China Sea.

Bathymetric range. —No depth record available for the only known specimen.

Remarks. —Both Mortensen (1948) and McKnight (1968) have suggested that *Anochanus sinensis* may be the female of *Aphanopora echinobrissoides* (see below). Because the only known specimen has never been completely figured, the drawings presented here have been based on the similar *Aphanopora* and the description given in Mortensen (1948).

Aphanopora de Meijere, 1902
Aphanopora echinobrissoides
de Meijere, 1902*
Fig. 12c

Geographic range. —Mortensen (1948) recorded the species from the Timor and Sulu Seas, and McKnight (1968) described two specimens from an area approximately 150 miles north of Norfolk Island.

Bathymetric range. —The Timor and Sulu specimens were found at 350 to 390 m, and McKnight's (1968) specimens were dredged from 710 m.

Remarks. —This species might actually be sexually dimorphic, with the females (possibly represented by *Anochanus sinensis,* see above) possessing an aboral brood cavity at the apical system. Therefore, the males would probably not have a sunken apical system, as figured by McKnight (1968). McKnight (1968) redescribed the species from material representing a range extension. However, his specimens were denuded tests, which prevented any speculation on the biology of the species.

Nannolampas Mortensen, 1948
Nannolampas tenera (de Meijere, 1902)*
Figs. 5b, 12d

Geographic range. —Known only from the Timor Sea.

Bathymetric range. —From a single "Siboga" station, at 390 m.

Remarks. —Mortensen (1948) assigned *Neolampas tenera* de Meijere, 1902 to a new genus, *Nannolampas,* because the latter species has a tetrabasal apical system. Nothing is known of the biology of *N. tenera.*

Tropholampas H. L. Clark, 1923
Tropholampas loveni (Studer, 1880)*
Fig. 12e

Geographic range. —South African coast, Cape Peninsula to Cape St. Francis (Mortensen 1948).

Bathymetric range.—Dredged from 135–350 m (Mortensen 1948).

Remarks.—The females of this species have a strongly developed aboral "marsupium" at the apical system, and the males have only a very slightly sunken apical system. In spite of the markedly different positions of the periproct, Mortensen (1948) thought that *Tropholampas* was closely related to *Anochanus* on the basis of common possession of an adapical brood cavity.

Acknowledgments

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